



Keys to the species of *Athesmia* Looss, 1899 (Digenea: Dicrocoeliidae: Dicrocoeliinae), with the description of a new species from the clapper rail, *Rallus longirostris* Boddaert (Gruiformes: Rallidae), from Galveston, Texas, U.S.A.

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Abstract

Eleven specimens of a previously undescribed species of *Athesmia* Looss, 1899 were recovered from six clapper rails, *Rallus longirostris* Boddaert (Rallidae), collected from November, 1984 through October, 1995 from the Galveston, Texas area of the Gulf of Mexico. Species of *Athesmia* can be divided into two body types based on the posterior extent of the ceca relative to the vitelline field (vitellarium): the attilae type where the ceca may be uneven, but they both extend at least to near the level of the posterior margin of the vitelline field, or more commonly surpass the vitelline field posteriorly and the heterolecithodes type where the cecum on the side of the vitelline field terminates well above the posterior margin of the vitelline field, usually near its anterior extremity, while the cecum opposite the vitelline field extends at least to the level of the posterior margin of the vitelline field, or more commonly surpasses the vitelline field posteriorly. *Athesmia ralli* n. sp. is assigned to the attilae type. The new species is most similar to *Athesmia butensis* Petri, 1942, but differs from this species by having a longer space from posterior testis to ovary (600–790 compared to less than 200), which represent a larger percentage of the total body length (7–8% compared to 2%) and a larger maximum egg size (47 by 29 compared to 42 by 25). The new species further differs from *A. butensis* by having a somewhat larger body, a longer forebody and the vitelline field reaches posteriorly to the posterior third of the body in the new species but is confined to the middle third of the body in *A. butensis*. A key to species also is provided.

Key words: *Athesmia ralli* n. sp., clapper rail, Digenea, Dicrocoeliidae, Dicrocoeliinae, Galveston, Gruiformes, parasite, keys to species, Platyhelminthes, Rallidae, *Rallus longirostris*, Texas, *Unilateralecithum*

Introduction

Athesmia heterolecithodes (Braun, 1899) Looss, 1899 was established by Braun (1899) with a very brief description (without illustrations) of *Distomum heterolecithodes* Braun, 1899 from the liver of a purple swamphen, *Porphyrio porphyria* Linnaeus (Gruiformes: Rallidae) (Syn. *Porphyrio madagascariensis* Sibley & Monroe), that had died at the Königsberg (now Kaliningrad) Zoological Gardens, Prussia (specimens originally imported from Madagascar). Jacoby (1899a, 1899b) provided more details of the morphology of this species from additional materials and included the common moorhen, *Gallinula chloropus* Linnaeus (Rallidae), from Germany (East Prussia) as an additional host. Later, Jacoby (1899c) more fully described and illustrated the species. In 1899, Looss erected *Athesmia* Looss, 1899 with *A. heterolecithodes* as the type species.

Yamaguti (1971) recognized 10 additional species (8 from birds and 2 from mammals) in the genus: *Athesmia attilae* Travassos, 1917 reported as being from *Attila cinerea* (Not a recognized species of bird; likely the grey-hooded Attila, *Attila rufus* Vieillot [Tyrannidae]), from Brazil (Travassos 1917); *Athesmia butensis* Petri, 1942 from the Galapagos hawk, *Buteo galapagoensis* (Gould) (Accipitridae), from the Archipiélago de Galápagos (Petri 1942); *Athesmia foxi* Goldberger & Crane, 1911 from the white-faced capuchin or monkey, *Cebus capucinus* (Linnaeus) (Cedidae), from the United States Public Health and Marine–Hospital Service (Goldberger & Crane 1911); *Athesmia jolleie* Schell, 1957 from the American kestrel or sparrow hawk, *Falco sparverius* Linnaeus (Falconidae), from Idaho, U.S.A. (Schell 1957); *Athesmia kassimovi* Feizullaev, 1961 from *P. porphyria* from the

Republic of Azerbaijan (Feizullaev 1961); *Athesmia parkeri* Pérez Vigueras, 1942 from the Jamaican fruit bat, *Artibeus jamaicensis* Leach (Phyllostomidae), from San Cristobal, Cuba (Pérez Vigueras 1942); *Athesmia pricei* McIntosh, 1937 from the dark-winged trumpeter, *Psophia viridis* Spix (Psophiidae), from the National Zoo, Washington D.C., U.S.A. (McIntosh 1937); *Athesmia reelfooti* Denton in Petri, 1942, first reported in Petri (1942), but described from *G. chloropus* from Tennessee, U.S.A. by Denton and Byrd (1942); *Athesmia rudecta* (Braun, 1901) from the plumbeous ibis, *Theristicus caerulescens* (Vieillot) (Syn. *Ibis caerulescens* Vieillot) (Threskiornithidae), from Brazil (Braun 1901); and *Athesmia wehri* McIntosh, 1937 from the sharp-tailed grouse, *Tympanuchus phasianellus* (Linnaeus) (Syn. *Pedioectes phasianellus* Linnaeus) (Phasianidae), from Montana, U.S.A. (McIntosh 1937). In a published summary of a thesis by Srivastva (1971), *Athesmia mehrai* **n. sp.** from India was listed but this species was neither described nor illustrated. As far as I can determine, this species was never formally described, and without access to representative specimens of this species it could not be considered in the present study.

The clapper rail, *Rallus longirostris* Boddaert (Gruiformes: Rallidae), is a relatively common (Although populations of these birds are decreasing, they are still considered as Red list of least concern), medium-sized wading bird that is most commonly found in the saltwater marshes throughout coastal North America. It is commonly found from Cape Cod to the Gulf of Mexico, the Caribbean and as far south as eastern Brazil on the east, and along the Pacific Ocean from California to Peru on the west (Walters, 1980; BirdLife International 2013).

The purpose of this study was to provide an up-to-date key to species of *Athesmia* and describe the new species.

Material and methods

Six clapper rails collected from November, 1984 through October, 1995 were examined for endohelminths. Specimens of *Athesmia* were relaxed in saline, studied alive, heat-killed under slight cover slip pressure, fixed in AFA, stained in Semichon's carmine, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam. Drawings were done with the aid of a Zeiss Universal compound microscope using a Pixera Pro 150ES imaging system and a drawing tube. Measurements are in micrometers (μm), and are given with the holotype followed by the ranges and means in parentheses. Two-dimensional measurements are given with the length before the width. Measurements of eggs were taken from normal-appearing eggs that were in a flat profile from the distal end of the uterus. Comparative measurements were taken from the original species descriptions unless otherwise stated. Specimens were deposited in the United States National Parasite Collection (USNPC) Beltsville, Maryland, U.S.A.

Results

Family Dicrocoeliidae Odhner

Subfamily Dicrocoeliinae Looss

Genus *Athesmia* Looss

Athesmia ralli **n. sp.**

(Figs. 1–3)

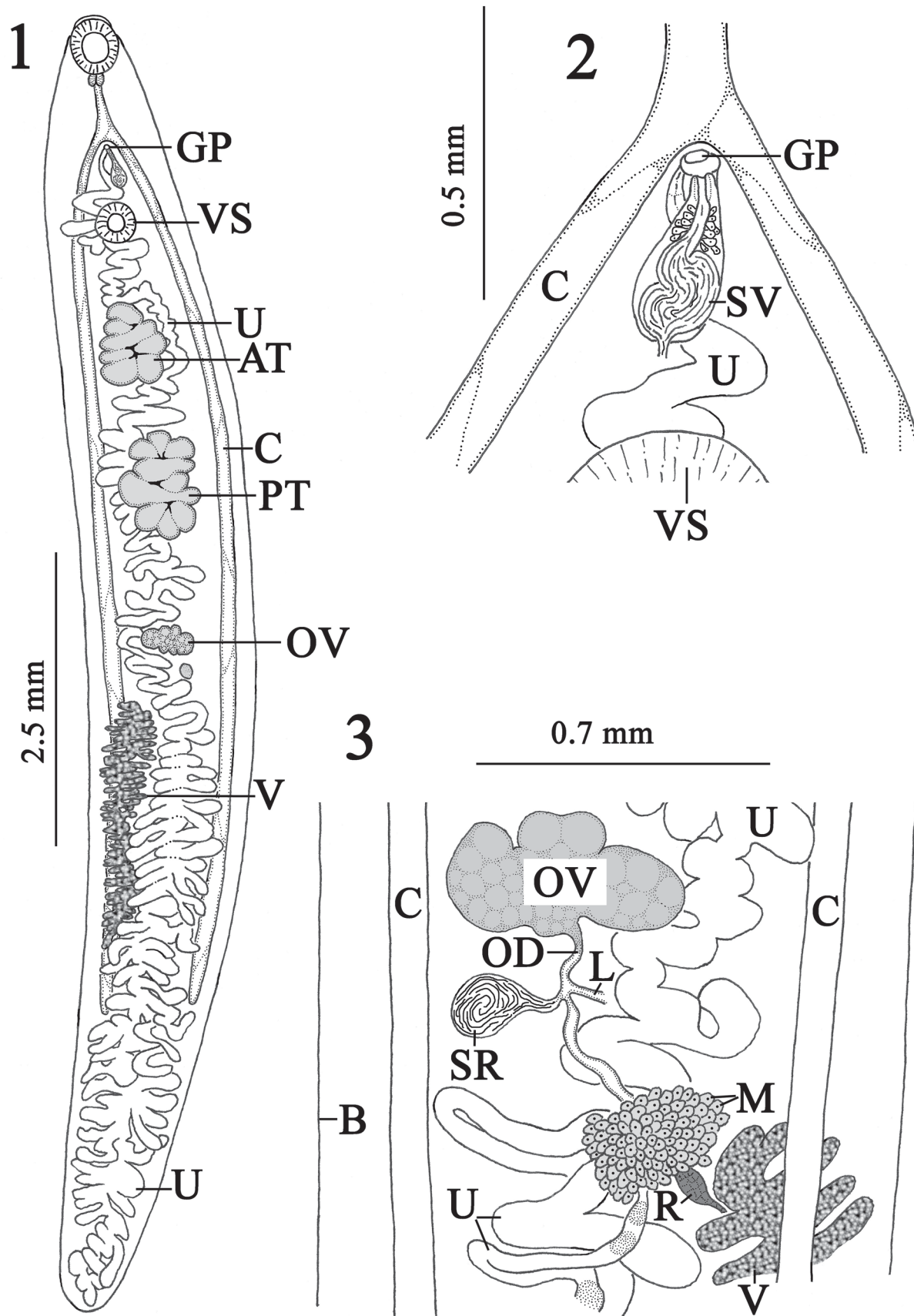
Type host: The clapper rail, *Rallus longirostris* Boddaert (Gruiformes: Rallidae).

Type locality: Galveston County, Texas, USA, 29 22' N, 94 34' W.

Site of infection: Liver

Deposited specimens: Holotype USNPC 107956.00; paratype USNPC 107956.00; voucher USNPC 78466.00.

Etymology: The species is named for the genus of the species of bird from which the new species was collected, *Rallus* Linnaeus.



FIGURES 1–3. *Athesmia ralli* n. sp. from the clapper rail, *Rallus longirostris* Boddaert (Gruiformes: Rallidae), from Texas. **1.** Ventral view of fully mature adult. **2.** Composite drawing of cirrus sac and seminal vesicle showing and cirrus and location of the genital pore, ventral view. **3.** Composite drawing of female genital complex, ventral view.

Description: Based on six adult specimens. With characteristics of genus. Body attilae type, relatively large, slender, elongate, aspinose, holotype 11,150 (range 8,978–11,150; mean 9,709) by 1,200 (1,200–1,450; 1,283); forebody 1,500 (1,475–1,573; 1,516) long, 13% (13–16%; 15%) of body length. Mouth subterminal, 410 (360–415; 385) by 388 (360–388; 369); preoral lobe present, 40 (20–40; 35) long; prepharynx absent; pharynx spherical to nearly circular, 110 (110–120; 115) by 130 (120–130; 125); esophagus long, 440 (400–440; 420) long, 4% (4–5%; 4%) of body length; cecal bifurcation near midlevel of forebody; ceca reaching well posterior to ovary, occupying 55% (55–70%; 62%) of postovarian space. Ratio of widths of oral sucker and pharynx 1:3.0 (1:2.3–1:3.5; 1:2.8). Ventral sucker located 1/6 distance down body, smaller than oral sucker to about same size, 380 (335–380; 365) by 395 (350–395; 378). Ratio of sucker widths 1:1.0 (1:0.9–1:1.5; 1: 1.1).

Testes lobed, tandem, situated near midlevel of upper 1/2 of body. Anterior testis 710 (470–990; 727) by 620 (540–620; 573); posterior testis 910 (480–910; 650) by 600 (600–720; 653). Cirrus sac medial, situated between cecal bifurcation and ventral sucker, enclosing short cirrus, reduced pars prostatica, short ejaculatory duct surrounded by prostate cells, and slightly coiled seminal vesicle, 330 (330–370; 343), 3% (3–4%; 4%) of body length by 150 (120–150; 134) wide. Genital pore immediately postbifurcal on midline of body.

Ovary lobed, posttesticular, situated a short distance posterior to midlevel of body, 230 (170–230; 210) by 420 (335–435; 400), postovarian space 5,723 (4,825–5,723; 5,141) long, 51% (51–54%; 53%) of body length. Seminal receptacle spherical, saccate, located immediately posterior and dextral to ovary, 184 (164–270; 206) by 150 (110–150; 133). Laurer's canal present, arising from oviduct across from seminal receptacle, proceeding sinistral towards midline of body, opening not observed. Single vitelline field (vitellarium) present on right side of body, locates in upper half of posterior half of body, dendritic, relatively large, 2,075 (2,075–2,250; 2,150) by 475 (175–475; 335), distributed along right cecum from level of oötype posteriorly to a short distance anterior to cecal ends in hindbody. Oötype some distance posterosinistral to ovary, located immediately anterior and dextral to anterior end of vitelline field. Uterus largely postacetabular, filling most of hindbody; descending limb proceeding posteriorly from ovary to posterior end of body, then turning anteriorly; ascending limb proceeding between vitelline field and ovary, then passing between the testes, proceeding anteriorly past ventral sucker to genital pore. Eggs numerous, operculate, 41–47 (40–47; 44) by 21–28 (21–29; 26) (n = 40) measured from distal end of uterus. Excretory vesicle I-shaped; excretory pore slightly subterminal.

Remarks: *Athesmia ralli* n. sp. has both of the ceca surpassing the level of the posterior margin of the vitelline field, terminating near the anterior extent of the posterior fifth of the body; thus it is assigned to the attilae type. The new species can be separated from all the other species assigned to the attilae type except *A. butensis* (*A. attilae*, *A. pricei*, *A. reelfooti*, *A. wehri*) by having eggs that were 40 or longer. The new species differs from *A. butensis* by having a longer distance from posterior testis to ovary (600–790 compared to less than 200), which represent a larger percentage of the total body length (7–8% compared to 2%), a larger maximum egg size (47 by 29 compared to 42 by 25), a somewhat larger body (8,978–11,150 compared to 7,300), a longer forebody (1,500–1,575, 13–16% of body length compared to 718, about 10%), vitelline field reaching posteriorly to the posterior third of the body rather than being confined to the middle third of the body as in *A. butensis*, and the new species is from rail from the Texas Gulf Coast rather than a hawk from the Archipiélago de Galápagos, Ecuador. The new species is somewhat similar to *A. kassimovi* in the heterolechithodes type, but further differs from this species by having a maximum egg size of 47 by 29 compared to 42 by 24, a larger space from the posterior testis to the ovary (695, representing 7–8% of body length compared to 124, about 3%), a longer cirrus sac (350, representing 3–4% of body length compared to 220, 6%), a longer intertesticular space (382, representing 3–4% of body length compared to 230, 6%), and *A. kassimovi* is from a swamp hen from the republic of Azerbaijan. Some authors (e.g. Panin 1984) consider *Unilateralecithum* Oshmarin, to be a synonym of *Athesmia*; however, more recent authors (Lamothe-Argumendo, *et al.* 2005; Pojmanska 2008) consider these two genera to be separate. These two genera can be distinguished because species of *Athesmia* have a preequatorial placement of the ovary that is in close proximity to the testes rather than being situated postequatorial, some distance away from the testes, and the vitelline field in species of *Athesmia* is largely confined to the middle third of the body rather than being situated in the posterior half of the body. I agree with Lamothe-Argumendo, *et al.* (2005) and Pojmanska (2008) in the separation of these two genera.

Keys based on two basic body types evident in the genus

Key to the two body types of *Athesmia* Looss, 1899

- 1a. Both ceca extending to level of posterior margin of vitelline field, usually surpassing it posteriorly *Athesmia attillae* Travassos, 1917 body type (Figs. 4–5)
- 1b. Cecum on side of vitelline field terminating anterior to posterior margin of vitelline field, usually near anterior margin of vitelline field; cecum opposite to vitelline field extending to level of posterior margin of vitelline field, usually surpassing it posteriorly *Athesmia heterolechithodes* (Braun, 1899) body type (Fig. 6)

Key to the species assigned to the attillae body type

- 1a. Eggs attaining a length of 40 or longer 2
- 1b. Eggs not attaining a length of 40 3
- 2a. Length of space from posterior testis to ovary 600–790, representing 7–8% of body length; maximum size of eggs 47 by 29 *Athesmia ralli* n. sp.
- 2b. Length of space from posterior testis to ovary less than 200, representing about 2% of body length; maximum size of eggs 42 by 25 *A. butensis*
- 3a. Body less than 5,000 long; eggs 28–30 by 14–17 *A. attillae*
- 3b. Body 7,000 or longer; eggs 31 by 18 or larger 4
- 4a. Ratio of pharynx width to oral sucker width 1:3.0 or less *A. pricei*
- 4b. Ratio of pharynx width to oral sucker width 1:4.0 or greater 5
- 5a. Intertesticular space length more than 700, representing about 7% of body length; eggs 33–38 by 23–25 *A. reelfooti*
- 5b. Intertesticular space length less than 500, representing about 4% of body length; eggs less than 33 by 21 *A. wehri*

Key to the species assigned to the heterolechithodes body type

- 1a. Eggs 36–42 long *A. kassimovi*
- 1b. Eggs 35 long or less 2
- 2a. Forebody relatively long, comprising about 20% of body length; eggs 25 by 16–18 *A. jolliei*
- 2b. Forebody relatively short, comprising less than 16% of body length; eggs 30 by 20 or larger 3
- 3a. Intertesticular space length more than 400, representing about 6% of body length; eggs 31 by 23 *A. heterolechithodes*
- 3b. Intertesticular space length less than 200, representing about 2% of body length; eggs 34 by 19–20 4
- 4a. Body 6,600–8,000 long; cirrus sac about 230, representing about 3% of body length *A. foxi*
- 4b. Body less than 5,000 long; cirrus sac about 265, representing about 6% of body length *A. parkeri*

Remarks: Species of *Athesmia* can be divided into two groups based on the posterior extent of the ceca relative to the vitelline field (vitellarium): the attillae body type where the ceca may be uneven, but they both extend at least to near the level of the posterior margin of the vitelline field, or more commonly surpass the vitelline field posteriorly (*A. attillae*, *A. butensis*, *A. pricei*, *A. ralli* n. sp., *A. reelfooti*, *A. wehri*) and the heterolechithodes body type where the cecum on the side of the vitelline field terminates well above the posterior margin of the vitelline field, usually near its anterior extremity, while the cecum opposite the vitelline field extends at least to the level of the posterior margin of the vitelline field, or more commonly surpasses the vitelline field posteriorly (*A. foxi*, *A. parkeri*, *A. heterolechithodes*, *A. jolliei*, *A. kassimovi*). The relative length of ceca commonly has been used in many digenean groups to distinguish genera and species. McIntosh (1937) used the length of the ceca relative to the vitelline field to separate *A. foxi* (“Intestinal ceca terminating near or before reaching level of caudal extremity of vitellarium”) from *A. pricei*, *A. attillae* and *A. wehri* (“Intestinal ceca terminating some distance posterior to the level of the caudal extremity of the vitellarium”) in his key to the species of *Athesmia* known at that time. This characteristic as used in the key to the two body types proposed herein appears to be a consistent and therefore it is an effective means to assist in the separation of species in the genus. The following characteristics were used in the keys proposed to species assigned to the two body types.

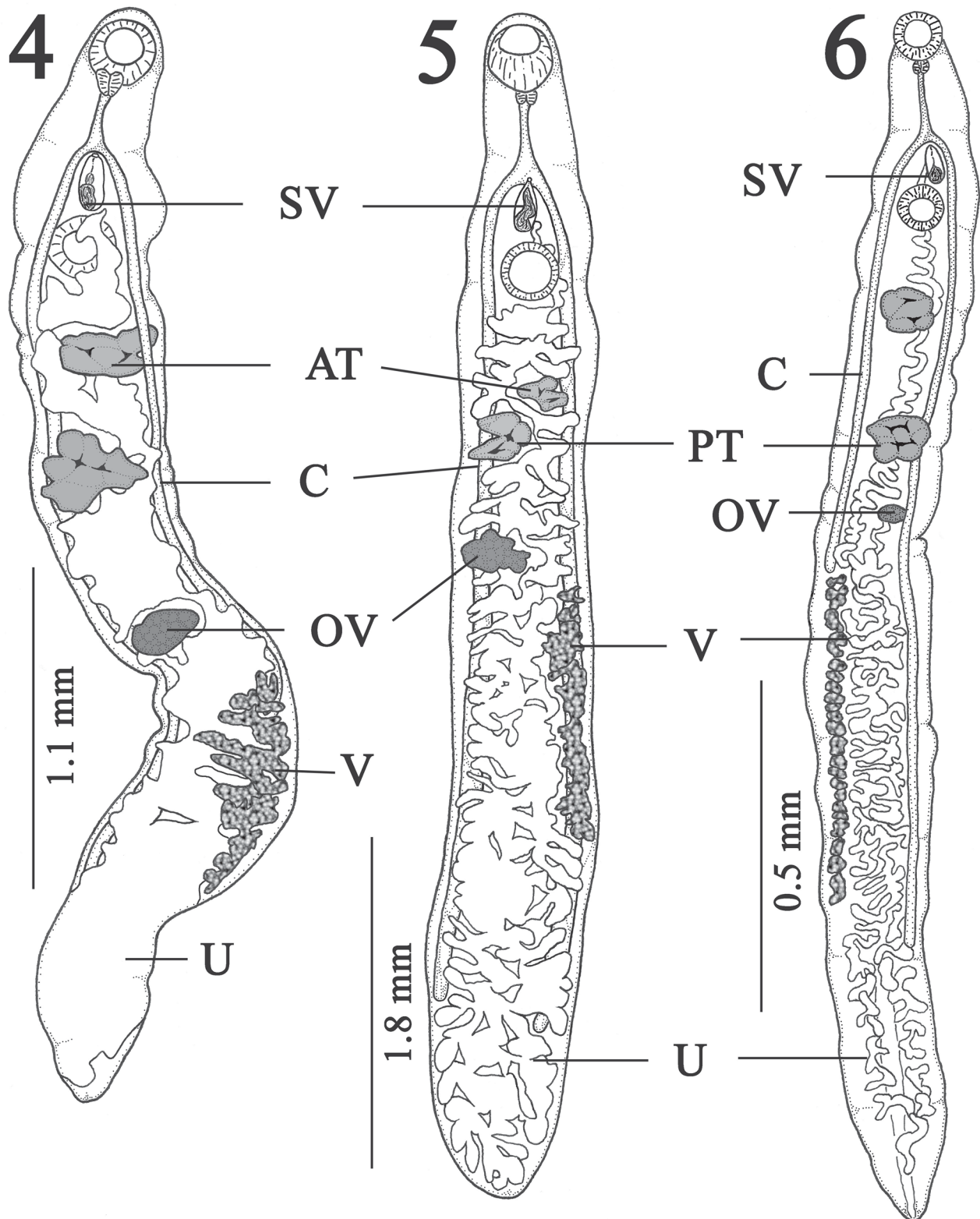
Egg size. In the keys for species assigned to both the attillae and heterolechithodes types, egg size was commonly used. Numerous authors (e.g. Freitas 1963; Mettrick & Dunkley 1968; Nasir & Díaz 1971, Dronen *et al.* 2012) have pointed out that egg size is one of the least variable characteristics in most groups of flukes for separating species. This appears to be the case in *Athesmia*, although egg sizes do sometimes overlap between

species, and occasionally the ranges of egg lengths and widths reported in descriptions can be relatively broad. Braun (1899) in the original description of *H. heterolechithodes* reported an egg size of 31 by 23, but in a redescription of this species based on the literature, Goldberger and Crane (1911) gave an egg size of 31–40 by 19–23. Egg size was used in couplet 1 to divide the species assigned to the attilae type into two groups, those where the eggs were 40 or longer and those where they were less than 40 long. Egg length also was used in couplet 2 along with the length of the space between the posterior testis and the ovary relative to body length to separate the new species from *A. butensis*; in couplet 3 along with body length to separate *A. attilae* from *A. pricei*, *A. reelfooti*, and *A. wehri* and in couplet 5 along with the length of the intertesticular space relative to body length to separate *A. reelfooti* from *A. wehri* in this same key. The new species further differs from *A. butensis* by having a somewhat larger body (8,978–11,150 compared to 7,300), a longer forebody (1,500–1,575, 13–16% of body length compared to 718, about 10%) and the vitelline field reaches posteriorly to the posterior third of the body in the new species but is confined to the middle third of the body in *A. butensis*. *Athesmia attilae* further differs from *A. pricei*, *A. reelfooti*, and *A. wehri* by having a different ratio of the width of the pharynx to the width of the oral sucker (1:3.5 compared to 1:2.7, 1:4.3 and 1:4.6 respectively). *Athesmia reelfooti* further differs from *A. wehri* by having a somewhat longer body (11,400 compared to 9,850), a shorter forebody (1,132, 10% of body length compared to 1,540, 16%), a shorter cirrus sac (240, 2% of body length compared to 400, 4%) and a longer postovarian space (6,226, 55% compared to 3,997, 41%). Similarly, egg size was used in couplet 1 of the key to species assigned to the heterolechithodes type to distinguish *A. kassimovi* from *A. jolliei*, *A. heterolechithodes*, *A. foxi* and *A. parkeri*; in couplet 2 along with the length of the forebody relative to the body length to separate *A. jolliei* from *A. heterolechithodes*, *A. foxi* and *A. parkeri* and in couplet 3 along with the length of the intertesticular space relative to body length to separate *A. heterolechithodes* from *A. foxi* and *A. parkeri*. *Athesmia kassimovi* further differs from *A. jolliei*, *A. heterolechithodes*, *A. foxi* and *A. parkeri* by having a different length of the postovarian space relative to body length (1,720, 43% of body length compared to 2,304, 52%; 5,260, 62%; 2,370, 34% and 2,260, 54% respectively) and from *A. jolliei*, *A. foxi* and *A. parkeri* by having a longer intertesticular space (272, 6% of body length compared to 100, 2%; 168, 2% and 90, 2% respectively). *Athesmia jolliei* further differs from *A. heterolechithodes*, *A. foxi* and *A. parkeri* by having the ovary wider than the mean width of the testes (1:0.8 compared to 1:2.4, 1:1.5 and 1:1.4 respectively). *Athesmia jolliei* further differs from *A. heterolechithodes* and *A. foxi* by having a longer cirrus sac relative to body length (230, 5% of body length compared to 250, 3% and 230, 3% respectively). It differs further from *A. heterolechithodes* and *A. parkeri* by having a longer space between the ovary and the posterior testis relative to body length (272, 6% of body length compared to 295, 3% and 180, 4%) and it has a smaller ratio of the width of the pharynx to the width of the oral sucker than *A. heterolechithodes* (1:3.5 compared to 1:4.8). *Athesmia heterolechithodes* further differs from *A. foxi* and *A. parkeri* by having a somewhat larger ratio of the width of the pharynx to the width of the oral sucker (1:4.8 compared to 1:4.0 and 1:3.3), a larger ratio of the width of the ovary to the mean width of the testes (1:2.4 compared to 1:1.5 and 1:1.2), and a longer postovarian space (5,260, 62% of body length compared to 2,370, 34% and 2,260, 54%). It further differs from *A. foxi* by having a shorter space between the ovary and the posterior testis relative to body length (295, 3% of body length compared to 410, 6%), and from *A. parkeri* by having a larger body (8,000–9,000 compared to 4,200) and a shorter cirrus sac relative to body length (250, 3% of body length compared to 265, 6% of body length).

Length of space from posterior testis to ovary. The length of the space from the posterior testis to the ovary relative to body length appears to be a relatively consistent characteristic in *Athesmia* and was used in couplet 2 of the key to species assigned to the attilae type along with egg length to distinguish the new species from *A. butensis*.

Body length. Body length was used only where there appeared to be a definite difference and where there were other corroborating differences. This characteristic was used in couplet 3 of the key to species assigned to the attilae type along with egg size to distinguish *A. attilae* from *A. pricei*, *A. reelfooti* and *A. wehri* and in couplet 4 of the key to the species assigned to the heterolechithodes type along with the relative length of the cirrus sac to separate *A. foxi* from *A. parkeri*. *Athesmia foxi* further differs from *A. parkeri* by having a shorter postovarian space relative to body length (2,300, 34% of body length compared to 2,260, 54%).

Ratio of width of pharynx to width of oral sucker. The ratio of width of the pharynx to the width of the oral sucker is commonly used to distinguish species in most fluke genera and was used in couplet 4 of the key to the species assigned to the attilae type to separate *A. pricei* from *A. reelfooti* and *A. wehri*. *Athesmia pricei* further differs from *A. reelfooti* and *A. wehri* by having a somewhat smaller body (8,000 compared to 11,400 and 9,850) and the ovary in *A. pricei* is wider than the mean testes width (1:0.5 compared to 1:1.0 and 1:1.1).



FIGURES 4–6. 4. *Athesmia attillae* “type”, apparently a dorsal view. After Travassos (1919), figure 5, representing the attillae body type. 5. *A. reducta* (likely *A. attillae*), ventral view. After Travassos (1944), plate 90, figure 4, representing the attillae body type. 6. *Athemia heterolechithodes*, ventral view. After Skajabin & Evranova (1952), figure 24, representing the heterolechithodes body type.

Abbreviations: AT, anterior testis; B, body wall; C, cecum; GP, genital pore; L, Laurer’s canal; M, Mehlis’ glands; OD, oviduct; OV, ovary; PT, posterior testis; R, vitelline reservoir; SR, seminal receptacle; SV, seminal vesicle; U, uterus; V, vitelline field; VS, ventral sucker.

Length of intertesticular space. The length of the intertesticular space is a commonly used characteristic to distinguish species in many genera of flukes, especially in those groups where the testes are tandem or nearly so. The length of the intertesticular space relative to body length was used along with egg size in couplet 5 of the key to the species assigned to the attilae type to separate *A. reelfooti* from *A. wehri*, and in couplet 3 along with egg size to distinguish *A. heterolechithodes* from *A. foxi* and *A. parkeri*.

Relative length of cirrus sac. The length of the cirrus sac is often used as a characteristic to separate species in fluke genera and it was used in couplet 4 of the species assigned to the heterolechithodes along with body size to separate *A. foxi* from *A. parkeri*.

An alternate key to the species assigned to *Athesmia* without regard to the two body types identified above

| | | |
|------|---|------------------------------|
| 1a. | Eggs attaining a length of 40 or more | 2 |
| 1b. | Eggs not attaining a length of 40. | 4 |
| 2a. | Maximum size of eggs 47 by 28; length of space from posterior testis to ovary 600–790, representing 7–8% of body length .. | <i>Athesmia ralli</i> n. sp. |
| 2b. | Maximum size of eggs less than 43 by 26; length of space from posterior testis to ovary less than 200, representing 2–3% of body length | 3 |
| 3a. | Cirrus sac 225 long, representing about 3% of body length; length of intertesticular space representing about 3% of body length | <i>A. butensis</i> |
| 3b. | Cirrus sac 220 long, representing about 6% of body length; length of intertesticular space representing about 6% of body length | <i>A. kassimovi</i> |
| 4a. | Eggs 30 or less long | 5 |
| 4b. | Eggs more than 30 long. | 6 |
| 5a. | Eggs less than 26 long | <i>A. jolliei</i> |
| 5b. | Eggs 28–30 long | <i>A. attilae</i> |
| 6a. | Maximum egg length 38; maximum egg width 25 | <i>A. reelfooti</i> |
| 6b. | Maximum egg length less than 34; maximum egg width 23 | 7 |
| 7a. | Space from posterior testis to ovary more than 700 long, representing 8% or more of body length; intertesticular space more than 300 long, representing 4% or more of body length. | 8 |
| 7b. | Space from posterior testis to ovary less than 500 long, representing 6% or less of body length; intertesticular space less than 200 long, representing about 2% of body length | 9 |
| 8a. | Ratio of pharynx width to oral sucker width about 1:4.6 | <i>A. wehri</i> |
| 8b. | Ratio of pharynx width to oral sucker width about 1:2.7 | <i>A. pricei</i> |
| 9a. | Eggs 31 by 23 | <i>A. heterolechithodes</i> |
| 9b. | Eggs 34 by 20 | 10 |
| 10a. | Body 6,600–8,000 long; cirrus sac about 230, representing about 3% of body length | <i>A. foxi</i> |
| 10b. | Body less than 5,000 long; cirrus sac about 265, representing about 6% of body length | <i>A. parkeri</i> |

Remarks: It is also possible to distinguish the 11 species in the genus using only the basic species characteristics available without consideration of cecal lengths relative to the vitelline field. It is interesting to note that each method of identification (with or without using the two body types defined above) provides a slightly different picture of at least some of the relationships between species. In the latter key where the two body types are not considered, *A. attilae* and *A. jolliei* are distinguished in the same couplet (couplet 5), suggesting a possible close relationship; however, in the two keys where cecal length relative to the vitelline field is considered, they each are distinguished in separate keys (*A. attilae* in the key to species in the attilae type; couplet 3 and *A. jolliei* in the heterolechithodes type; couplet 2), suggesting that these two species are not as similar (closely related). Similarly, *A. butensis* and *A. kassimovi* are distinguished in the key where relative length of ceca is not considered in couplet 3, while *A. butensis* is distinguished from *A. ralli* n. sp. in couplet 2 in the key to species assigned to the attilae type, and *A. kassimovi* is distinguished in couplet 1 in the key to species assigned to the heterolechithodes type. *Athesmia ralli* n. sp. (couplet 2), *A. reelfooti* and *A. wehri* (couplet 5), and *A. pricei* (couplet 4) are all distinguished in the key to species assigned to the attilae type, while *A. heterolechithodes* (couplet 3), *A. foxi* and *A. parkeri* (couplet 4) are distinguished in the key to species assigned to the heterolechithodes type.

This poses the question of which choice of characteristics provides the best (most realistic) resolution to separate out these species that provides the best indication of the relative closeness of species in the key? Dronen *et al.* (2012) provided a discussion of some of the shortcomings in developing keys to species in *Mesocoelium* Odhner, (Digenea: Mesocoelidae), but did not consider in any detail the influence of ranking characteristics (i.e.

relative cecal length above egg size) on reflecting possible relationships (closets to more distant) between species in the key. Species keys are tools of convenience in taxonomy, but they should also reflect as best we can the most likely relationships between species. Although egg size can be a very consistent and useful characteristic for separating species in many groups, eggs sizes within species are generally a relatively precise characteristic and are sometimes too similar to be used effectively, and in some cases (e.g. Cyclocoeliidae; Mesocoeliidae) in-utero growth and development can generate large, misleading ranges in length and width of eggs. I consider the relative length of the ceca to be a broader characteristic than egg size, and in *Athesmia* cecal length in relation to the vitelline field appears to be a reasonably consistent characteristic and thus it should be ranked above other more precise characteristics (e.g. egg size) in keys to species in the genus. Whereas, both approaches to develop keys discussed above will allow species determination in the genus, in my opinion the two keys based on relative cecal length to distinguish between the two body types likely are more accurate.

Discussion

Braun (1901) named *Lyperosomum rudentum* Braun, 1901, from the plumbeous ibis, *Theristicus caerulescens* (Vieillot) (Syn. *Ibis caerulescens* Vieillot) (Threskiornithidae), that had been collected from Brazil, but did not provide a complete description or illustrations of this species until 1902. Although the species, as described and illustrated, conforms in most respects to members of Dicrocoeliidae (e.g. cirrus sac well developed, located anterior to ventral sucker; two testes in anterior half of body; genital pore median, opening in area of cecal bifurcation; ovary in anterior half of body, located posterior to testes; uterus with descending and ascending limbs forming numerous coils that occupying most of hindbody; terminal aspect of uterus running between testes), the distribution of the two vitelline fields in this species is unique for Dicrocoeliidae in that they are more extensive than previously described for members of the family (ranging from the level of the posterior end of the esophagus posteriorly to the posterior third of the hindbody). Travassos (1919) noticed this unusual distribution of the vitelline fields and established the genus *Lyperotrema* Travassos, 1919 with *L. rudenta* as the type species, largely based on this more extensive distribution of the vitelline fields. Later, Travassos collected additional materials from the gall bladder of the plumbeous ibis in Brazil and found specimens of dicrocoeliids that along with the same vitelline field distribution, matched *Lyperostomum rudentum* as described by Braun (1902). However, Travassos also encountered some specimens in this species of ibis that in most respects resembled *Lyperostomum rudentum* as described by Braun, but were like species of *Athesmia* by having only one vitelline field present on one side of the body. Travassos apparently considered these two vitelline distributions from specimens from the same species of bird host in Brazil as an expression of the natural variability in a single species and reassigned *Lyperotrema rudenta* to *Athesmia*, as *Athesmia rudenta* (Travassos 1941), effectively placing *Lyperotrema* in synonymy with *Athesmia*; an interpretation that was accepted by Yamaguti (1971) and later by Pojmańska (2008). In my opinion, the two vitelline distributions observed by Travassos (1941, 1944) are distinct and the specimens of “*A. rudenta*” of Travassos that have two vitelline fields likely represent the *L. rudenta*, as originally described by Braun (1902). Based on the presence of two vitelline fields and their more extensive distribution, these specimens cannot be assigned to *Athesmia*. I consider Travassos (1919) to have been correct in establishing a new genus of Dicrocoeliidae to accommodate the specimens of Braun (1901) and that *Lyperotrema* should be reinstated in Dicrocoeliinae with *Lyperotrema rudenta* as the type species as originally proposed by Travassos (1919). The specimens collected by Travassos in which there was a single, less extensive vitelline field should be assigned to *Athesmia* (Based on both ceca surpassing the posterior margin of the vitelline field posteriorly, as reported by Travassos 1944, these specimens would be assigned to the attilae type, probably represent *A. attilae*). However, the measurements of these specimens provided by Travassos 1944 may be unreliable in determining the species represented, as we cannot be assured that specimens from more than one genus (e.g. *Lyperotrema* and *Athesmia*) were not mixed or that the synonymies proposed by Travassos (1944) for *A. rudenta* did not result in more than one species being used for the measurements reported (e.g. *A. attilae*, *A. butensis*, *A. pricei*). It is interesting to note that figure 67 of *Lyperosomum lobatum* Railliet, 1900 in Braun (1902) is a species of *Athesmia*; however, there are no details concerning the length of the ceca to determine the body type. Using the key to the species assigned to *Athesmia* without regard to the two body types provided above the *L. lobatum* of Braun (1902) is most similar to *A. ralli* n. sp. by having a similar egg size (41–45 by 22–28 compared to 40–47 by 23–29), but differs in having a

smaller length of the space between the ovary and the posterior testis (about 150, 2% of body length compared to 600–790, 7–8%).

In the case of *A. attillae*, the original description by Travassos (1917) was minimal, contained no illustrations or information on deposited type materials, and provided only a vague statement that appeared to indicate that both ceca extend posteriorly to near the posterior end of the body (“extending up until near posterior end”). Travassos (1941) synonymized *A. attillae* with *A. rudecta* and later (Travassos 1944) provided an illustration of what was labeled the “type” of *A. attillae* (N. 1.429a; plate 92, figure 1). He also provided additional measurements for what appears to represent a type series (N. 1.429a, b, c; N. 1.430) for this species. Unfortunately, the specimens used to describe *A. attillae* by Travassos (1944) do not correspond to those used in the original description in 1917 (e.g. measurements, eggs 30–34 by 19–22 compared to 28–30 by 14–17; body length 2,930–4,140 compared to 3,500–4,000; oral sucker width /pharynx width 1:2.4 compared to 1:3.5) and may represent a different species. Although Travassos (1917) originally described the ceca as extending posteriorly to near the posterior end of the body in *A. attilla*, the figures of the “type” from the 1919 (Travassos 1919; figure 5) and 1944 (Travassos 1944; plate 92, figure 1) are unclear as to the posterior extent of the ceca (see figure 4 of the current study). However, additional figures of specimens identified as *A. reducta* (e.g. Travassos 1944; plate 90, figure 4) that correspond to the attillae body type and presumably represent *A. attillae* (see figure 5 of the current study) or a similar species shows the ceca extending well posterior to the vitelline mass. It is possible that examination of the original specimens used to describe *A. attillae* might yield a different interpretation of cecal length that would result in the reassignment of *A. attillae* to the heterolechithodes type (See *A. heterolechithodes*, figure 6 of the current study).

Acknowledgments

I would like to thank Mrs. Patricia Pilitt, United States National Parasite Collection, Beltsville, U.S.A. for allowing me access to specimens of *Athesmia* from the USNPC and for her assistance in depositing specimens of the new species at the museum. This study was funded by a grant from the Schubot Exotic Bird Research Center, the Texas Veterinary Center, Texas A&M University.

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